Myotis thysanodes.   By Michael J. O'Farrell and Eugene H. Studier

Myotis thysanodes Miller, 1897

Fringed Myotis

Myotis thysanodes Miller, 1897:80. Type locality Old Fort Tejon, Tehachapi Mts., Kern Co., California.

CONTEXT AND CONTENT. Order Chiroptera, Family Vespertilionidae, Subfamily Verpertilioninae. The genus *Myotis* includes approximately 80 species (Wilson and LaVal, 1974). Three subspecies of *Myotis thysanodes* are recognized.

M. t. aztecus Miller and G. M. Allen, 1928:128. Type locality San Antonia, Oaxaca, Mexico.

M. t. thysanodes Miller, 1897:80, see above.

M. t. pahasapensis Jones and Genoways, 1967:231. Type locality 6 miles N Newcastle, Weston Co., Wyoming.

DIAGNOSIS. A member of the large-eared group of *Myotis*, it is the only species with a well developed fringe of hairs on the posterior edge of the uropatagium (Fig. 1). This species, although similar to *Myotis evotis*, is larger, except in ear size. The skull is larger and has a well developed sagittal crest; however, when compared with a bat of similar size (*M. velifer*), *M. thysanodes* has a more slender and delicate skull (Fig. 2). There is no metaloph and the protoconule and paraloph are usually absent on the first and second molars, which represents an extreme simplification not observed in other American species of *Myotis*. The robust calcar is not distinctly keeled. A detailed description is contained in Miller and Allen (1928).

GENERAL CHARACTERS. Ranges of external body measurements are summarized as follows (Miller and Allen, 1928; Hall and Kelson, 1959; O'Farrell, unpublished): length of head and body 43 to 59 mm; length of tail 34 to 45 mm; length of ear 16 to 20 mm; length of forearm 40 to 47 mm. Fur ranges in color from yellowish brown to darker olivaceous tones, with little difference between dorsal and ventral surfaces. Color varies geographically, with a tendency towards darker coloration in northern populations (Miller and Allen, 1928). Sexual dimorphism has been found, with females exhibiting significantly larger head and body, as well as forearm lengths (Williams and Findley, 1979).

DISTRIBUTION. The geographic distribution is shown in Fig. 3. In general, this species is found in western North America from British Columbia to Veracruz and Chiapas, with a disjunct population in the Black Hills of Wyoming and South Dakota. Recent observations have extended the range of *M. t. pahasapensis* (Jones and Choate, 1978) and for *M. t. thysanodes* (Williams, 1968; Armstrong, 1972; Boyce, 1980). The fringed myotis primarily occurs at middle elevations (1,200 to 2,100 m) in desert, grass and woodland habitats, but is found to 2,850 m in spruce-fir habitat in New Mexico (Barbour and Davis, 1969; Findley et al., 1975). Jones (1965) described *M. thysanodes* as occurring almost exclusively in evergreen forests in the Mogollon Mountains of New Mexico and Arizona. Populations occur at low elevations along the West Coast (Orr, 1956). The species occurs in sagebrush-grasslands in Washington (Williams, 1968). Collec-

tions in the fall have been made at water troughs in the creosote-burro bush association of southern Nevada (O'Farrell, unpublished). There is no fossil record.

FORM. Physical properties of the wing membranes of *M. thysanodes* were determined by Studier (1972) and compared to several other species of bats that utilize different foraging behaviors. The wing membranes are moderately thick (0.024 mm), possess moderate elasticity (12.9 mm/kg), and have a high puncture strength (9.37 kg/mm). Resistance to puncture is a characteristic of bats that forage by gleaning from the ground or in areas of thick or thorny vegetation.

General flight characters may be static as in aspect ratio or dynamic as in wing loading (O'Farrell and Studier, 1975). Aspect ratio (wing span²/area of wings) for 100 adult *M. thysanodes* was relatively low (6.00); after adult size was reached, little variation was found. A low aspect ratio indicates precision, low speed flight, which is expected for a gleaning foraging strategy. Wing loading (body weight/total flight surface) varies daily as well as seasonally. Wing loading of individuals returning to the roost after feeding and watering was significantly greater than that for individuals emerging from the roost in the evening. Prepregnant and post-lactating wing loadings were significantly lower than for pregnant and lactating conditions; this was true even excluding the weight of embryos. Embryo-free live body weight followed the same trend.

The baculum of *M. thysanodes* was described by Krutzsch and Vaughan (1955). It was characterized as dumbbell-shaped, averaging 0.77 mm in length, and with a ventral groove.

FUNCTION. A detailed analysis of thermoregulatory patterns within a maternity roost was described by Studier and O'Farrell (1972). Thermal patterns and levels of thermoregulation of the summer colony (April to September) were characterized as highly variable. At ambient temperatures (T_a) of 24°C or less, individuals could be classed either as conformers (poikilothermic response) or regulators (homeothermic response). During pregnancy and lactation there were significantly more regulators, although there was an average of 17% conformers; however, during lactation, 50% were conformers. Within the pregnant group, mid-pregnancy was characterized by a significant number of regulators, whereas early and late pregnant groups approached 40% conformers. Throughout the study, 16 to 25% of all individuals exhibited the phenomenon of "shifting" from regulation to conforming and vice versa. *Myotis thysanodes* becomes partially hy-
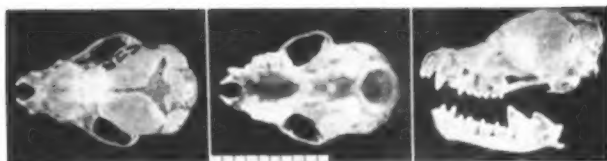

FIGURE 1. Skull and lower jaw of *Myotis thysanodes* on deposit at the Natural History Museum of Los Angeles County. Photographs by Barbara Stewart.

FIGURE 2. Dorsal view of the uropatagium of *Myotis thysanodes* illustrating the posterior fringe. Photograph by Barbara Stewart.
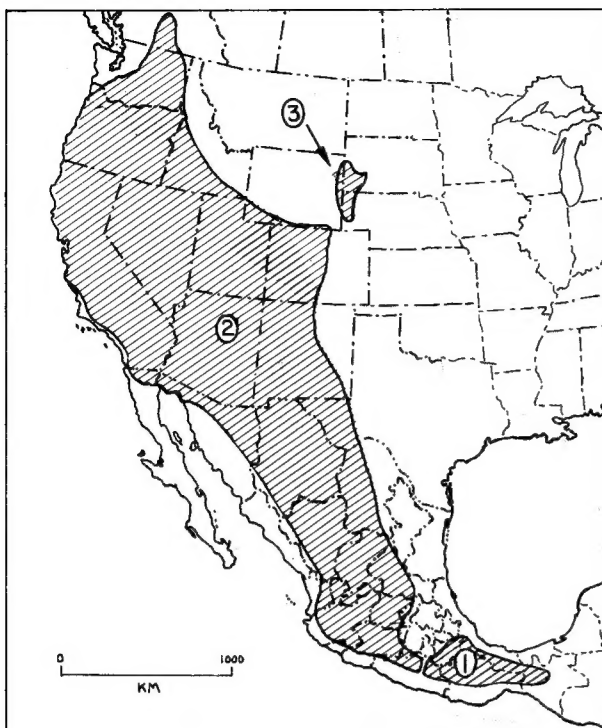
FIGURE 3. Geographic distribution of *Myotis thysanodes* in North America (modified from Hall and Kelson, 1959). 1, *M. t. aztecus*; 2, *M. t. thysanodes*; 3, *M. t. pahasapensis*. Illustration by T. Blair O'Farrell.

perthermic at temperatures above 24°C, and fully hyperthermic at T_a's above 32°C.

This species apparently thermoregulates if the energy demand required for regulation is not excessive. Regulating, lactating bats maintain their body temperature (T_b) significantly lower than pregnant or post-lactating regulators. The weight of embryos does not relate to the level of controlled T_b in regulators. The relation between T_a and T_b of regulators is curvilinear and predictive equations for each reproductive condition were given in Studier and O'Farrell (1972). Behavioral thermoregulatory features such as microhabitat selection may be of greater survival value to this species than physiological thermoregulation.

Minimum T_b required for flight averages 24.3°C. The ability to fly at reduced T_b, as well as other physiological patterns given below, suggest that this species migrates to suitable habitat and is periodically active throughout the winter. Associated with low temperature flight, Hirshfeld and O'Farrell (1976) described warming rates and thermal mapping for *M. thysanodes*. After initiation of flight, rectal temperatures average 24.9°C whereas chest muscle and interscapular temperatures tended to be higher, 27.3° and 28.9°C, respectively. Rectal temperatures were probably lower due to shunting of blood away from the periphery and areas posterior to the diaphragm. What is surprising is the maintenance of metabolically active tissues below 29°C.

Preliminary information on fall metabolism was reported for bats just prior to the autumnal exodus from the maternity roost (O'Farrell and Studier, 1970). The thermoneutral zone occurred between T_a's of 32.5°C and 34.5°C with a minimum metabolism of 1.74 cm³ of oxygen/g/h. The critical thermal maximum (T_a at which short-term exposure proved lethal) was 44.5°C. A transition from a homeothermic to a non-homeothermic metabolic response to the standard T_a gradient was evident by late September.

A more thorough, long-term examination of intra-roost metabolic response was reported by Studier and O'Farrell (1976). Multiple regression analysis revealed that fat levels, spleen or adrenal weights, and relative age had no significant effect on metabolic response. Reproductive status, however, significantly affected metabolic parameters. The best predictors of oxygen consumption were T_a and the T_b to T_a differential. Equations for oxygen consumption, weight specific oxygen consumption, breathing rate, heart rate, oxygen pulse, and evaporative heat loss for each reproductive condition for both regulators and con-

formers were presented by Studier and O'Farrell (1976). Likewise, T_a at which all these physiological responses reach minimal levels in regulators were also predicted.

Thermoregulating *M. thysanodes* appear to use two strategies for energy conservation. Lactating regulators maintain a controlled T_b approximately 2°C lower than that of pregnant regulators. A corresponding drop in weight-specific oxygen consumption occurs during lactation. Post-lactating regulators, on the other hand, maintain a controlled T_b identical to that of pregnant regulators. A reduction in weight specific oxygen consumption occurs during post-lactation but is accounted for by a change in thermal conductance, which reduces heat loss. An alternate strategy to the above is to conform, which likewise reduces energy expenditure.

Diurnal weight loss within the roost was examined by Studier et al. (1970). Weight loss for individuals ranged from 9.0 to 21.8% ($\bar{X} = 15.8$), whereas weight loss of grouped bats ranged from 10.1 to 11.5% ($\bar{X} = 10.9$). Weight loss during the first 3 hours of roosting was more than twice as great as during the remaining 11 hours within the roost. The initial rapid weight loss was thought to be primarily due to fecal and obligatory urine loss, independent of the roost environment. During the last 11 hours in the roost, weight loss was primarily pulmocutaneous water loss, which is environment dependent. Weight loss at which half the bats died was 31.7% of initial body weight. Evaporative water loss was modeled in relation to T_a and correlated with breathing rate (Studier and O'Farrell, 1976). Predictive equations were supplied for both regulators and conformers for each reproductive state.

Gross body composition fluctuated significantly throughout the maternity roost period (O'Farrell and Studier, 1976). Embryo-free live body weights were significantly different in all reproductive stages and are listed in order of increasing value: prepregnant, post-lactation, pregnant, lactation. Changes in water content were identical in trend and accounted for the primary differences in body weight, although lean dry biomass during pregnancy and lactation was significantly greater than in prepregnant or post-lactation stages. When compared to percent water, organic and mineral compartments displayed reciprocal fluctuations. Mineral content reached a peak in pregnancy, whereas organic percentages were lowest during lactation. In adults, percent mineral increased with increasing age categories based on tooth wear.

Autumn fat deposition and gross body composition were described by Ewing et al. (1970) and later examined in detail for the full tenure of *M. thysanodes* in the maternity roost (O'Farrell and Studier, 1976). Fat indices (g fat/g lean dry weight) were low and constant from early spring until late summer. Prior to the fall emigration from the maternity roost, fat levels increased rapidly. Fat levels obtained for each year were different, indicating a certain flexibility, probably dependent on environmental conditions. Maximum fat indices in 1969 reached 0.73 (Ewing et al., 1971), whereas in 1970 they did not exceed 0.50 (O'Farrell and Studier, 1976). Body fat had a caloric content of 9.4 kcal/g. Fatty acid analysis indicated that oleic acid was the most common (Ewing et al., 1970); this represents a common situation for animals preparing for hibernation.

Spleen and adrenal weights were also examined by O'Farrell and Studier (1976). Splenic weight increases were significant for post-lactating individuals, although definite increase was also noted during pregnancy and lactation compared to prepregnant levels. The authors hypothesized that these increases were related to erythropoiesis. Adrenal weights were relatively stable through the year except during lactation when they almost doubled in size. The great increase in physiological stress during this period was suggested as the causative factor.

Energy utilization and water requirements of captive *M. thysanodes* in the fall were reported by O'Farrell et al. (1971). An average of 5.05 kcal/day was ingested and 0.47 kcal/day egested, thus an assimilation efficiency of 90.8%. Water gained (ingested and metabolic) averaged 2.77 cm³/day and water lost (egested and evaporated) averaged 2.86 cm³/day, representing a water turnover of almost half the total body weight.

The minimal energy costs of pregnancy and lactation were determined through bomb calorimetry of known-age young bats and embryos (Studier et al., 1973). Energy demand during pregnancy was hyperbolic, with the initial rapid increase occurring at 34 days prior to birth. This corresponded to late pregnancy when mothers were no longer homeothermic, thereby reducing maintenance energy costs. Energy utilized for reproduction during late embryo growth averaged 78 cal/day, whereas lactation required an average of 346 cal/day.

Roosting time and energy budgets have been calculated by

Studier and O'Farrell (1976). Estimated maintenance metabolism varied by reproductive condition for both conformers and regulators. The latter ranged from 1.09 to 1.41 kcal/day with pregnancy accounting for the high and lactation the low value. Individuals that shift thermoregulatory response can reduce energy costs by almost half by conforming at T_a's of 16°C and regulating at all higher T_a's. At present, no estimates of time and energy costs of flight are available.

ONTOGENY AND REPRODUCTION. The only detailed description of the reproductive cycle is for northeastern New Mexico (O'Farrell and Studier, 1973). Females did not copulate until after leaving the maternity roost in the fall. Ovulation, fertilization and implantation occurred between 28 April and 15 May. Gestation was between 50 and 60 days in length. Parturition began on 25 June and concluded by 7 July. No data are available for males, although young of the year showed no evidence of testicular activity. The reproductive cycle for *M. thysanodes* elsewhere in its range is poorly known. Lactating bats with immature young have been collected during the first 2 weeks of July throughout the southern portion of the western United States, as well as one northern California location (Miller and Allen, 1928; Dalquest, 1947; Cockrum and Ordway, 1959; Easterla, 1973). Barbour and Davis (1969) reported mid-pregnant bats near Colorado Springs on 18 June and a late pregnant bat in Chihuahua on 28 June. Only one young per year is the norm (Cockrum, 1955; Barbour and Davis, 1969). Evidently there is little variation in the timing of reproduction throughout the range of the species.

Prenatal and postnatal growth were described in detail by O'Farrell and Studier (1973). Predictive equations were provided for weight, forearm and crown-rump lengths. In addition, postnatal predictive equations were given for weight, length of forearm, wing span, length of fifth digit, total length, and lengths of head and body, tail, tibia and ear. At parturition, fetuses were large and precocial; they averaged 54% of the total length of adults and 22% of the weight of adults. The eyes were open and pinnae erect shortly after birth. Neonates were pink for approximately 1 week, during which time skin pigmentation commenced, followed by hair growth within pigmented areas. Young were capable of limited flight at 16.5 days of age. Agility of flight steadily increased until flight became indistinguishable from that of adults by 20.5 days of age. Similarly, young were indistinguishable from adults, for all measured parameters, by 21 days of age. After this age, young of the year could be distinguished only by lack of epiphysial closures.

Body composition fluctuated predictably through postnatal growth (O'Farrell and Studier, 1973). Percent water decreased significantly from birth to adult size, with a concomitant significant increase of both percent organic and mineral components. Fat index increased from 0.08 at birth to 0.29 at 22 days of age, which is greater than twice the fat level of lactating adults. Spleen and adrenal weights (g/kg fat free live weight) did not change significantly through growth.

ECOLOGY. This species may be found from low desert scrub associations up to fir-pine associations (see Distribution). Oak and pinyon woodlands appear to be the most commonly used vegetative associations (Roest, 1951; Hoffmeister and Goodpaster, 1954; Cockrum and Ordway, 1959; Jones, 1965; Findley et al., 1975). Several colonies, as well as isolated occurrences over water holes, are known for low desert scrub associations in southern Arizona (Cockrum and Ordway, 1959), Texas (Easterla, 1973), and Nevada (Burt, 1934; Birdspring Range, Clark Co., O'Farrell, unpublished). Williams (1968) found this species in a sage-grassland in Washington. All desert and steppe areas within the range of *M. thysanodes* were within an hour flight from forested or riparian areas.

Roost sites have been found in caves (Burt, 1934; Commissaris, 1961; Baker, 1962; Easterla, 1966, 1973), mine tunnels (Cahalane, 1939; Cockrum and Musgrove, 1964), and buildings (Orr, 1956; Musser and Durrant, 1960; Studier, 1968). Any of these sites may serve as either day or night roosts (Pearson et al., 1952). Nothing has been reported concerning specific microhabitat requirements within caves or tunnels. O'Farrell and Studier (1973) described specific roost sites within an attic complex for a large maternity colony. This species tended to roost in the open in tightly packed clusters. The sides of ceiling joists were preferred sites, although cracks between beams were also utilized.

Fringed myotis are known to migrate, although little is known about the magnitude of movements or destination of all migrators. Hoffmeister (1970) documented the difference in distribution of summer and winter colonies in Arizona. Studier and O'Farrell

(1972) speculated, based on physiological performance, that fall migrations were of short distances to lower elevations or more southern areas where the bats could be periodically active in winter. Spring migration into a maternity roost was rapid, occurring from mid- to late April (O'Farrell and Studier, 1975). The spring influx took less than a month. The population remained stable until September, and then declined rapidly during fall migration. The uniformity of population movements was reflected in the synchronized narrow span of parturition. During the summer, adult males are totally segregated from the maternity colony. Easterla (1973) made similar observations in Texas.

In the population studied by O'Farrell and Studier (1975), virtually all females examined were pregnant. Sex ratio at birth was equal. Population structure changed significantly with the cessation of lactation; young males left the roost prior to young females, and by early fall only adult females remained. Age structure (based on tooth wear) was skewed heavily towards young animals.

Monthly changes in relative abundance of mist-netted bats were reported by Jones (1966). In addition, relative abundance values were obtained over a 10 year period by Jones and Suttkus (1972), and for 5 years by Easterla (1973). Populations fluctuated over a 10 year period resulting in a small net gain in abundance (Jones and Suttkus, 1972); population lows occurred in 1962 and 1963, whereas peak abundance occurred in 1965.

Generalized food habits have been described by Black (1974). Utilizing moth scale density and percent frequency of occurrence of moth and beetle parts in fecal pellets, he determined that *M. thysanodes* ate mostly beetles (73% frequency). Observations indicated relatively slow, highly manuverable flight with foraging occurring in proximity to the vegetative canopy.

An examination of the above works on various aspects of the ecology of *M. thysanodes* reveals a rather consistent list of coexisting species: *Myotis evotis*, *M. volans*, *M. californicus*, *M. leibii*, *M. lucifugus*, *M. velifer*, *M. yumanensis*, *M. auriculus*, *Eptesicus fuscus*, *Pipistrellus hesperus*, *Lasionycteris noctivagans*, *Plecotus townsendii*, *Idionycteris phyllotis*, *Euderma maculatum*, *Lasiurus borealis*, *L. cinereus*, *Antrozous pallidus*, *Tadarida brasiliensis*, and *Tadarida macrotis*. Such a large list reflects the widespread geographic and altitudinal range of this species and combines information from netting at water sources and from roost sites. Trophic niche partitioning for many of these species was discussed by Black (1974). A detailed comparison of differences, both ecologically and physiologically, has been presented for *M. thysanodes* and *M. lucifugus* in a series of articles by O'Farrell and Studier (see Literature Cited).

A variety of acarine and insect ectoparasites have been collected from *M. thysanodes*. Bradshaw and Ross (1961) reported the following: Spinturnicidae—*Spinturnix carloshoffmanni*; Argasidae—*Trombicula myotis*; Cimicidae—*Cimex pilosellus*; Nycteribiidae—*Basilia forcipata*; and Ischnopsillyidae—*Myodopsylla collinsi*. Whitaker and Easterla (1975) collected *Spinturnix americanus* and *B. forcipata*. Krutzsch (1955) reported *Ichoronyssus* (Dermanyssidae), as well as *Spinturnix* and numerous unidentified nycteribiids. In addition, Rudnick (1960) found *S. carloshoffmanni* and Usinger (1966) reported *Cimex latipennis* and *C. incrassatus*. Certain ectoparasites are found on specific regions of the body: *Spinturnix* and *Ichoronyssus* on the wing membranes, *Ornithodoros* on the sides and back of neck and body, *Cimex* on the forearm, and nycteribiids on the furred portions of the body. Cain and Studier (1972) examined 17 fringed myotis but found no endoparasites. In a later study, they found two individuals (5.0%) to be parasitized by the cestode, *Vampirolepis gertschi* (Cain and Studier, 1974).

BEHAVIOR. The known activity period extends from April through September (see Ecology). Females prepare physiologically for hibernation during the post-lactation period of late summer and early fall, prior to migration. Hibernation may be periodically interrupted throughout the winter (see Function).

Nightly activity has been determined by mist net records (Jones, 1965). Bats were captured from shortly after sunset to approximately 4.5 hours from sunset. The majority of individuals were captured between 1 and 2 hours from sunset. Wind and precipitation generally did not affect visible bat activity, but did reduce numbers captured. Nightly activity associated with maternity roosts is less revealing (O'Farrell and Studier, 1973). Females left the roost at sunset and returned en masse near dawn. However, two to 10 adults were always present within the roost during the period of lactation. Precipitation did not affect nightly emergence (O'Farrell and Studier, 1975).

Periodic changes in roost sites within a maternity roost ap-

pear to be common both in caves (Baker, 1962) and buildings (Studier and O'Farrell, 1972; O'Farrell and Studier, 1973). Within buildings, intraroost movements are associated with thermoregulatory as well as reproductive behavior. The attic studied had a high ceiling and was relatively open, furnishing a wide range of microclimates, particularly along a vertical thermal gradient. Fringed myotis hung in tight clusters on the west side of the roof prior to noon. As the afternoon sun heated the west side of the roof and temperatures near the roof exceeded 40°C, the bats moved to the east side of the roof and positioned themselves farther down the beams. During the hottest parts of the day, individuals would take short flights in order to reduce T_b. On a seasonal basis, bats tended to use the warmer rooms, but in the month prior to the fall migration bats began to congregate in the coolest room of the attic.

This species seems easily disturbed by human presence. However, prior to parturition females become even more secretive and are virtually impossible to approach. Birth, which was observed for one individual (O'Farrell and Studier, 1973), occurred in a head down posture, and the placenta was consumed. After parturition, the neonates were deposited in a cluster separate from adult roost sites. Baker (1962) observed similar behavior in Carlsbad Caverns. Adults would periodically fly to the neonate cluster, suckle a young, then return to the original roost site. Some of the intraroost movements during lactation were accompanied by a transfer of some young to new sites in close proximity to adult locations. Nonvolant young were periodically dislodged and fell to the floor. In such cases, the young would begin vocalizing a distress call. An adult would fly to the young, allow it to attach to a nipple, then return it to the cluster. Older individuals were capable of climbing the wall and returning to the original roost. At night the young were tended by a few females which suckled and retrieved individuals when necessary.

Mean flight speed within an "artificial mine tunnel" was estimated at 13.8 km/h or 8.6 mph (Hayward and Davis, 1964).

GENETICS. The karyotype of *M. thysanodes* is identical with those of all other *Myotis* species examined for North America (Baker and Patton, 1967). For the two individuals examined, $2n = 44$ and $FN = 50$. The autosomes consist of 4 pairs of metacentrics and 17 pairs of acrocentrics. Both the X and Y chromosomes are submetacentrics.

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